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What are algal turfs? Towards a better description of turfs

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ABSTRACT: The use of standardised classifications, or operational definitions, is essential if different researchers are to measure and compare similar entities. In the marine realm, algal 'turfs' are increasingly reported to be globally expanding at the expense of kelps and canopy-forming algae. However, ecological research about the underlying drivers of this shift is limited by a vague and inconsistent definition of what exactly a turf is. In order to stimulate more effective descriptions of 'turfs' and facilitate communication of research outcomes and comparisons across studies, we reviewed the use of the term turf in ecological studies of temperate coasts and coral reefs and (1) identified the main types and distribution of algal assemblages known as 'turfs', (2) examined the descriptions of turfs so that we may recognise some general characteristics, including those contingent on environmental conditions; and (3) offered character descriptions that could improve communication and comparisons. These descriptors centre on reporting information on the morphology, height, density of thalli, the amount of sediment trapped in turfs and a description of the area covered by turfs, including their patchiness and persistence. Our review recognised these as common attributes that could be usefully described across a wide range of circumstances and provide insights into the ecology of turfs and their interactions with other assemblages in a community. The use of common descriptors would provide the term 'turf' with greater scientific value.

KEY WORDS: Algae · Coral · Definition · Epilithic · Rock · Temperate · Turf-forming

INTRODUCTION

Ecologists have long sought to identify the broad structural classifications that describe vegetation across landscapes in comparable ways (Lavorel et al. 1997). One of the most commonly used classifications centres on morphological descriptions of both terrestrial (e.g. tall and low shrublands, closed and open forests, grasslands and woodlands) and marine vegetation (e.g. canopy-forming algae, algal crusts, foliose algae). Whilst the identification of major vegetation types, layering, composition and succession has also been based on plant physiology, taxonomy and biogeography, morphological classifications originated as a way to qualitatively describe vegetation across locations of different taxonomic composition and biogeography.

In the marine realm, the term 'turf' is becoming increasingly used (Fig. 1) to identify a typically low-lying (several mm to cm tall) layer of algae. The increasing use of this term reflects a growing interest in understanding the ecology of turfs themselves, as

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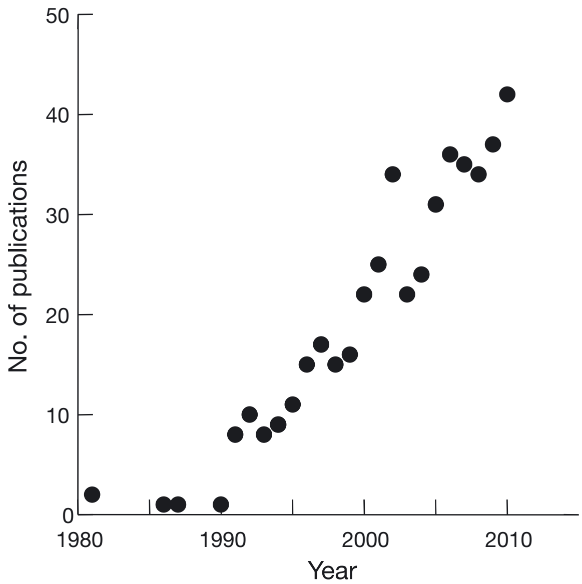

Fig. 1. Number of papers per year that used the term 'turf' in publications about 'alga' (1980–2010 inclusive)

well as their effects on other assemblages (e.g. Airoldi 2000, Britton-Simmons 2006, Bulleri & Benedetti-Cecchi 2006, Gorman & Connell 2009). Algal turfs are major components of intertidal and subtidal rocky coasts of all latitudes (i.e. tropical, temperate, polar) and central to fundamental descriptions of patterns of benthos at local (Virgilio et al. 2006) through biogeographic scales (Connell & Irving 2008). Turfs are fundamental to the dynamics of many coastal systems (Airoldi et al. 1995 and references therein); they are components of both short-term (e.g. early succession, Edwards 1998, Irving & Connell 2006) and long-term dynamics (e.g. degradation of coral reefs and kelp forests, Carpenter 1990, Airoldi 2003, Diaz-Pulido & McCook 2003, Gardner et al. 2003, Gorman et al. 2009, Perkol-Finkel & Airoldi 2010), including ecological forecasts of climate changeability (Connell & Russell 2010, Connell et al. 2013). Turfs are expanding globally on rocky coasts and coral reefs and are increasingly used as indicators of human-made disturbances (see reviews by McCook et al. 2001, Connell 2007, Airoldi et al. 2008).

The term 'turfs' is used in 2 general ways. Firstly, it is used to designate short, densely branched algae that occur as part of a broader community. This use is analogous to the use of 'trees' or 'shrubs' and does not necessarily require further elaboration because 'turf' is used as part of a general description of a community, usually qualitative, and is not the focus of study. The second involves 'turfs' as an integral part of a study. We consider that if 'turfs' are integral to the study (e.g. ecology of turfs) we need a basis on which to compare studies. In this latter case, the term 'turf' does not provide a common basis on which we can currently understand their identity and ecology.

The usefulness of ecological definitions comes from their common recognition across wide-ranging circumstances, and ongoing demonstration that they provide clearer insights into ecological phenomena. This review, therefore, aims to (1) identify the main types and distribution of algal assemblages known as 'turfs', (2) review the descriptions of turfs so that we may recognise some general characteristics of turfs to (3) produce a standard set of characters (e.g. relevant morphological or ecological traits) that could be used as descriptors of turfs. It does not seek to identify the various functions of turfs (i.e. functional-group hypotheses). Our intention is to provide a basis for the future recognition and description of turfs that allows more meaningful communication and comparisons of their ecology among researchers and across their systems of study. A more standardised set of descriptors would provide the term 'turf' with greater scientific value.

DEFINITIONS OF TURFS

The term 'turf' is primarily used in agriculture to describe lawn-like landscapes that are low lying (mm to cm tall) and are defined as a layer of grass plus roots and associated earth in grasslands (Webster and Oxford Dictionaries). Braun-Blanquet (1932) was among the first to use 'turf' to designate a layer morphologically similar to a turf of grass that occurs in a variety of natural settings, including terrestrial forests. He also called this stratum a 'moss layer', which has similar meaning to the term the 'muscinal layer' (Kühnemann 1970) that describes terrestrial mosses (Corradini & Clement 1999). Braun-Blanquet (1932) did not quantitatively define the morphological characteristics of either 'turf' or 'moss'. As a result of his pioneering intertidal and subtidal sampling, Gislén (1930) recognised alternate growth forms of benthic marine organisms and considered that organisms of similar form could form an association that facilitates their growth. He named small, delicate forms composed of branching filaments or blades with branches <1 mm diameter and up to 10 cm tall the 'Parvosilvida' (Latin: small forest), including genera such as *Cladophora*, *Enteromorpha* and *Polysiphonia*. He called the association produced by such forms 'parvosilvosa', but did not associate it with a layering classification. Thus, turf, muscinal and parvosilvosa are different terms for the same type of vegetation, and Gislén (1930) appears to be the first to attempt a quantitative definition of marine turfs.

While noting that 'turf' occurred in many marine habitats, later investigators often chose to either not precisely describe what they called turf, or to use descriptors different from those of Gislén (1930). Stewart (1982, p. 45) recognised the term 'turf' as a convenient category for algae that 'form mats of small algal thalli in warm temperate and tropical regions, although workers describing these associations often explicitly indicate differences in composition and structure'. The use of the word 'mat' in conjunction with turf is interesting and relevant. According to Webster's Dictionary, a 'mat' is something that is 'interwoven or tangled into a thick mass' and describes some, but not all turfs. Indeed, Hay (1981) distinguished between 'mats', filamentous species that trap sediment and have vertical and horizontal uprights; and 'turfs', tightly packed, colonial aggregates of 1 to many macroalgal species with upright branches >0.5 cm tall. An additional difficulty with 'mats' is that it is often applied to tangled, intertwining, attached or unattached bunches of algae (e.g. *Ulva* spp., filamentous algae) on soft bottoms, particularly when they get bound to sediments (e.g. Neumann et al. 1970). Although numerous past definitions of turfs have pointed to sediments as a structural constituent of algal turfs (e.g. Stewart 1983, Kendrick 1991, Airoldi et al. 1995), this description may not characterise a substantial proportion of algae that have come to be known as 'turf' attached to hard substratum.

Filamentous turfs have been of particular focus on coral reefs where they are the most widespread and the main source of primary productivity and mediate transitions of habitat from coral to algal domination (Bellwood et al. 2004). Most tropical research recognises turfs as a ubiquitous and multispecies assemblage of short algae (i.e. 1 to 10 cm height) that is primarily comprised of filamentous algae (for a review, see Steneck 1988), but a subset of researchers use the alternative term 'epilithic' algae to describe turfs (n = 79 papers from 1983 to 2010, mostly from Australia). The term 'epilithic' is derived from 'epi' (i.e. upon) and 'lithic' (i.e. rock) and has obtained widespread usage from studies of freshwater algae since the 1970s (Moore 1974). The term was initially used by Hatcher & Larkum (1983, p. 61) to describe algal communities, 'primarily small, forming low turfs or mats' on coral reefs and is often abbreviated EAC for epilithic algal communities.

The uncertainty that marine ecologists have with using the more commonly used term 'turf' is illustrated with ongoing terminological difficulties that coral reef researchers have with this alternative term, 'epilithic'. In an attempt to clarify a subset of EAC, another term, viz. 'epilithic algal matrix' (EAM), was coined to explicitly recognise the large amount of organic matter associated with 'turf-forming filamentous algae' (Wilson et al. 2003). The use of such unique terminology may insulate such publications from the broader readership. Some coral reef researchers have resisted such isolating terminology by incorporating both 'turf' and 'epilithic' into their communications (e.g. 'eplithic algal turfs'; Bonaldo & Bellwood 2011) or by retaining the use of 'turf', but listing 'epilithic' as a keyword only (e.g. McCook 2001).

CURRENT USE OF THE TERM 'TURF'

We reviewed the definitions of turfs from a subset of 109 papers published from 2005 to 2010 inclusively (6 yr), focussing on algal turfs from a variety of temperate and coral reef habitats (ISI search on the titles and abstracts using combinations of the terms 'turf', 'alga' and 'seaweed'): 26% of these papers provided no description of any phylogenetic, morphological or ecological characteristic of the assemblages which had been referred to as turfs, 46% gave some very limited description (generally the broad morphology, i.e. filamentous, calcareous articulated or coarsely branched), and only 28% of the papers provided a clearer description of what was referred to as turf, generally including an indication of their phylogenetic composition, morphology or size and more rarely of some peculiar ecological traits (e.g. spatial dominance, high productivity, ability to trap sediments).

Most turfs are either not defined or are poorly defined (Table S1 in the Supplement at www.int-res.com/articles/suppl/m495p299_supp.pdf). When lists of species are provided, many are nominated as turfs without reference to any one particular morphological, ecological or systematic definition. Our synthesis also revealed substantial variation in what assemblages were referred to as turfs. In papers offering a description, the majority were classified as filamentous turfs (68%), followed by corallines (24%) and mixtures of filamentous and foliose algae (8%). The variation in the phylogenetic composition and morphology of turfs is notoriously large (Hay 1981, Stewart 1982, Airoldi 2001), and our review confirms that the term 'turf' is unlikely to refer to a single type of alga, but represents several types of micro- and macroalgae which share an extensive low-lying morphology. Over time, these algae have come to be classified as 'turfs' without explicit consideration of their taxonomy, morphology and ecology. Further, implicitly or explicitly, turfs often act as a 'catch-all' for numerous small taxa that are difficult to identify, but this approach is unlikely to provide clearer insights into their ecology.

While most researchers simply use the term 'turf' to describe what the assemblage looks like, there has been some development towards consideration of the properties that distinguish turfs from other assemblages (e.g. Hay 1981, Stewart 1983, Steneck 1988, Airoldi et al. 1995, Airoldi 2001). Nevertheless, there continues to be vagueness, and lack of commensurability among studies hampers communication of research outcomes, particularly in ways that enable meaningful comparisons. The recognition of 'turfs' in one study and place, therefore, may not necessarily be recognised in another study and place. This would be particularly problematic for studies attempting to understand the ecology of turfs. This uncertainty impacts a large literature of nearly 500 articles. Of the top 50 cited articles using 'turf' and 'alga' in marine science over the last decade (ca. 1992–2011), 45 articles were ecological, and of these, 77% were about the role that turfs play in communities of which most (60%) were about their connection with human-made disturbances.

MAIN CHARACTERISTICS OF ASSEMBLAGES REFERRED TO AS TURFS

The only unifying description for 'turfs' is that they are usually composed of loosely to densely aggregated algal thalli, <15 cm tall, composed of 1 or more species and covering areas on the order of m^2 or larger (Table S1). This description is not a very useful account of 'turfs'. The following sections seek to identify relevant descriptors that, in our opinion, would be more useful.

Species composition

Algae that have been considered to form turfs include a variety of groups, among them diatoms, cyanobacteria, Chlorophyta, Rhodophyta and Phaeophyta. Turfs have long been recognised as being comprised of numerous species at all spatial scales (i.e. globally, locally and in any one sample). Indeed, when reported, the multi-species composition of turfs is a frequently described characteristic (i.e. 14%). Nevertheless, some turfs have also been reported as monospecific in composition, such as those comprised of articulated or geniculate corallines (e.g. *Corallina officinalis*; Blockley & Chapman 2008) that cover large areas with occasional interspersion of other species (Kelaher 2002) or those comprised of some invasive filamentous species such as the rhodophytes *Acrothamnion preissii* and *Womersleyella* (*Polysiphonia*) *setacea* which have invaded the Mediterranean sea with dense and persistent virtually monospecific stands (Airoldi et al. 1995, Piazzi & Cinelli 2000, Nikolic et al. 2010).

Turfs can also be highly variable morphologically even within species. This variability not only occurs over geographic scales (Murray & Bray 1993) but also at local scales where different morphologies are intermixed in the same turf (Stewart 1982, Airoldi 2001). Since turfs are often comprised of numerous species that are difficult to identify, it is not surprising that authors tend to use other ways to describe them.

Height

Turfs have been defined as 'short' or 'low lying' algae. These descriptors have referred to vastly different heights (0.5 to 10 cm) and may refer to, for example, thalli that are heavily grazed (<0.5 to 1.0 cm), filamentous (i.e. <1.0 to 2.0 cm) or to the thick branches of geniculate corallines (<10.0 cm).

Historically, some of the more extreme heights ranged from Neushul & Dahl (1967), who implied that turf is generally <10 cm tall, to Dahl (1972), who limited turfs to thalli that were 0.1 to 3 cm tall and thick, and Hay (1981), who defined them as >0.5 cm tall with no upper limit. Defining 'short' or 'low lying' as a function of the height of surrounding algae may not be generally useful. The height of algae described as 'turf' in some regions can approach the height of algae described as canopies (e.g. *Cystoseira* 20 to 30 cm in the Mediterranean; Benedetti-Cecchi et al. 2001).

Morphology

The most commonly classed morphologies are filamentous (corticated and uncorticated), foliose and calcareous articulated.

Filamentous turfs may be dense aggregations of erect thalli or an intertwined matrix of erect and prostrate branches (Fig. 2A). They may be formed by small red algae, chain-forming diatoms, cyanobacteria, microalgae and juvenile stages of macroalgae.

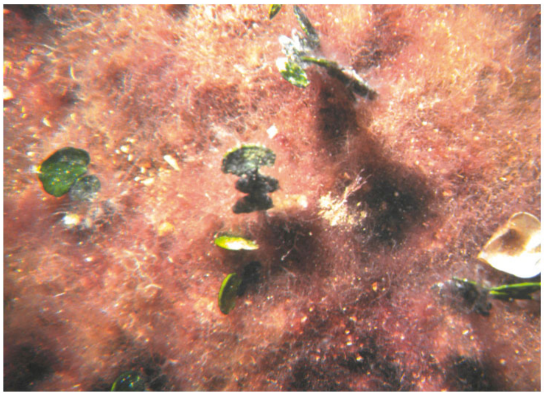

Fig. 2A. Filamentous turfs in 13 m (Livorno, Italy, Mediterranean) comprised of the thin, intertwined branches of the filamentous invasive rhodophyte *Womersleyella* (*Polysiphonia*) *setacea* that monopolize hectares of rock. They form persistent covers of ~1 to 5 cm tall turfs which trap large amounts of sediment. This photo spans 3 to 4 cm

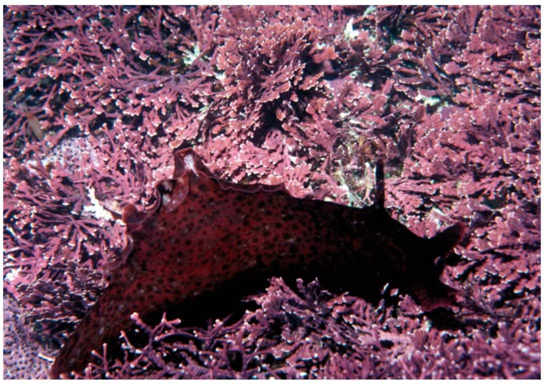

Fig. 2B. Thick thallus turf on rock at 12 m depth within a giant kelp forest. It is composed of the stiff, intertwined branches of the geniculate coralline *Calliarthron cheilosporioides.* The turf is persistent, ~10 to 15 cm tall, with only thin, patchy layers of sand beneath when the photo was taken. The sea hare moving over the turf is ~20 cm long. Carmel, California (USA)

Fig. 2. Examples of the kinds of systems that have been classified as turfs

Fig. 2C. Thick thallus turf on carbonate benches in the low intertidal zone of ‘Ewa Beach, Hawaii (USA). Sampling showed that the turf was composed of at least 24 algal taxa, with *Laurencia*, *Asparagopsis* and *Hypnea* the most common genera. The turf is persistent, ~3 to 5 cm tall, with a thin layer of sand beneath. The bench in the foreground is ~3 m long

Fig. 2D. Filamentous, ephemeral turfs on large intertidal boulders. They comprise microalgae and juvenile stages of macroalgae. The boulder is about 1 m large. Hammonnasset Beach State Park (Connecticut, USA)

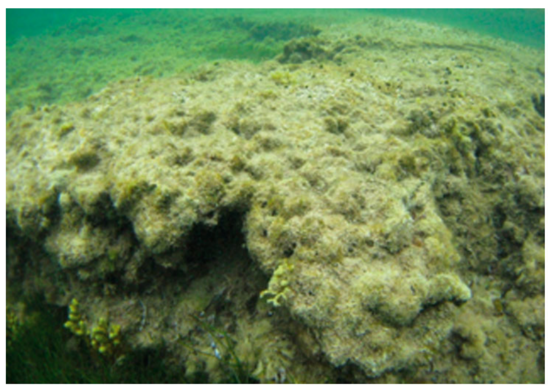

Fig. 2E. Filamentous turfs at 8 m depth (Adelaide Metropolitan coast, South Australia) primarily composed of thin upright branches of filamentous *Feldmannia* spp. with interspersed *Polysiphonia decipiens* that monopolize 100s of metres. They form persistent covers of ~1 to 5 cm tall turfs which trap large amounts of sediment. The photo spans 10 m foreground by 20 m from front to back

Some species can show considerable morphological plasticity, with variable growth forms (from solitary to densely aggregate) and degree of compaction associated with varying levels of disturbance and stress in the environment (Hay 1981). Filamentous forms have been observed to adopt a foliose (i.e. 'fan-shaped') form within a week of protection from herbivores (Diaz-Pulido et al. 2007). The same species may grow as a stolon and produce runners (see 'Growth form and reproduction'), or occur as individuals, loose turfs and tight turfs depending upon the habitat in which they occur (Taylor & Hay 1984).

Turfs with thick thalli (>1 mm), usually resulting from extensive cortication, can form persistent aggregations (Fig. 2B), such as the geniculate corallines *Laurencia* and *Dictyota.* Thick thalli turfs form visually different aggregations (Fig. 2C) due primarily to differences in branch stiffness that overlap in densely packed aggregations (see 'Density of thalli').

Growth form and reproduction

Many turf species spread vegetatively via rhizomes and can propagate via vegetative fragmentation (Neushul & Dahl 1967, Dahl 1972, Foster 1972, Hay 1981, Airoldi et al. 1995, Nikolic et al. 2010). Hay (1981) defined the shape of turfs as being affected by (1) the number of uprights per length of prostrate, (2) their degree of branching and (3) the extent to which the branches are connected. He defined turfs as 'clonal assemblages' and suggested that turf species possess both prostrate and upright branches. Suitable descriptions, therefore, may include the presence of prostrate 'rhizomes' from which upright branches arise and their 'lateral connections' (i.e. branches that may have grown together). Clonal turfs may also spread via the production of new uprights from expanding holdfasts.

Importantly, Neushul & Dahl (1967), Dahl (1972) and Foster (1972) noted that many species nominated as turfs are not clonal, for example most coralline algae and *Sargassum* spp. that form intertidal turfs in Hawaii (Abbott & Huisman 2004, M. S. Foster pers. obs). The individual thalli of prostrate or upright branches may be foliose, but together they may consolidate into 'turfing' morphology.

Density of thalli

Whilst authors frequently emphasise the density of thalli (usually meaning branches, as individual algae are often impossible to visually distinguish in a turf) as a character of turfs, none of the reviewed papers provided a description of this character, apart from being 'dense'. The extent to which fronds are packed together is variable, but in general they tend to be tightly packed so that individual fronds touch each other (Dahl 1972, Hay 1981). Over 600 thalli cm^{-2} have been observed for some species (Foster 1972). Whilst many species that form turfs can also occur as sparse aggregations or as individuals, individuals in such loose configurations are not generally named 'turfs'. The degree of packing appears to be a key characteristic used to separate 'turf' from other algal assemblages (numerous examples listed by Hay 1981, Taylor & Hay 1984).

Branch stiffness

We recognise that branch stiffness or vertical rigidity can be an important characteristic or descriptor of turfs as, among other things, it can affect sedimentation and habitat for associated animals. Stiffness ranges from lax branches of filaments through stiff branches of geniculate corallines. Lax branches (e.g. diatoms, filamentous *Polysiphonia*) often do not stand up on their own; they lie over the intertidal rock at low tide (e.g. Fig. 2D, Hay 1981) or are buoyed up on subtidal rock. Stiff branches retain their vertical form independently of emersion.

Association with sediments

Many turfs trap and accumulate sediments (Fig. 2E). Indeed, sediments are often considered a constituent component of their presence, persistence and structure (Airoldi & Virgilio 1998). Whilst any structure that slows down water motion tends to 'trap' sediments (e.g. kelp forests trap sediments), the striking characteristic for turfs is the large amount of sediment trapped relative to their small size (Airoldi 2003, Nikolic et al. 2010).

Coral reef ecologists coined the term EAM to explicitly recognise the large amount of organic matter associated within 'turf-forming filamentous algae'. On temperate coasts, the sediment bound within turfs has been of concern to those observing the displacement of canopy-forming algae by turfs (for review, see Airoldi et al. 2009). Turfs may inhibit the recruitment of taller algae (Gorman & Connell 2009, Perkol-Finkel & Airoldi 2010) through the inability of their spores to attach to solid surfaces (Norton & Fetter 1981, Airoldi 1998). They may also, especially in the intertidal zone, facilitate the recruitment of some kelps by providing suitable microenvironments and a refuge from grazing for microscopic stages (McConnico & Foster 2005, Schiel & Thompson 2012).

Coverage and persistence

The horizontal coverage of turfs ranges from several times greater than their height to extensive carpet-like aggregations. Isolated individuals or clumps of a few individuals are not recognised as turfs. For example, the growth form of algae can vary from individual thalli, often epiphytes, to dense clumps and up to small colonies (*Pterosiphonia pennata*; Lauret 1974).

Some species can be both extremely pervasive, colonising a large range of habitats, and persistent over time to a range of disturbances (e.g. *Womersleyella setacea*; Airoldi et al. 1995, Piazzi & Cinelli 2000, Nikolic et al. 2010). Others may appear to be absent, but instead have lost most of the uprights above holdfasts or rhizomes so that they persist to regrow during better times (e.g. facultative annuals/ephemerals, Neushul & Dahl 1967, Foster 1972).

Turfs can have a marked seasonality such that they are sparse to absent in one season, but in another form dense extensive carpet-like aggregations. Ephemeral blooms can cover large areas of substratum, e.g. the flats and crests of coastal and inshore fringing coral reefs, often blanketing small corals. Such carpet-like forms may be only loosely attached to the substratum (e.g. *Hydroclathrus clathratus*), but to emphasise their carpet-like form they have been referred to as 'mat-forming algae' (Hauri et al. 2010). There is something pervasive about the ecology of carpet-like aggregations, sometimes termed 'mat-forming algae', that induces comparison of their properties across tropical and temperate systems (e.g. Connell et al. 2013).

PROTOCOL FOR DESCRIPTIONS OF ALGAL TURFS

If we are to understand whether 'turfs' have a set of general properties that enable their comparison among studies and locations, we need a common basis on which to describe their 'turfs' and their variation. If turfs have useful properties that distinguish them from other algae, then seeking to specify which broad traits (e.g. which subset of species, thallus thickness) will occur within a particular set of environmental conditions is a constructive endeavour. This work may provide a predictive capacity for anticipating future environments and new localities with different turf species and attributes.

Our review suggests that we are not yet in a position to evaluate this possibility because turfs are too poorly described to enable commensurable comparisons. In addition to species composition and relative abundance, we encourage the following:

Morphology: describe their morphological characteristics.

Height: provide measurements of the range and average height of the turf.

Growth form and reproduction: describe their form of growth and connectedness.

Density: describe the density of branches at the surface of the turf. Quantify, if possible, otherwise estimate distance between branches. State whether branches are loose to tightly packed, whether the branches are intertwined, matted or separated and their average distance apart.

Sediment: describe the amount of associated sediment (none, thin, thick), its depth, and composition (e.g. silt, sand, mud).

Cover: describe the average area occupied by turfs (m^2) and its patchiness (i.e. lawn versus mosaic of large or small patches).

Temporal persistence: estimate the length of time the turfs persist.

Not all of these characteristics may usefully describe any single type of turf in a particular location, but including such components as part of their description would provide ecologists with a more coherent understanding of turfs among studies and in different environments.

CONCLUSION

Whilst 'turfs' are often used as a category to describe components of a community, they are increasingly becoming the focus of ecological study in their own right. If we are to understand their ecology and assuming that they have some generalizable properties, we need an agreed set of categorical descriptions that act as a common basis from which different researchers can measure and compare similar entities. We accept that turfs are often not given to taxonomic identification, making some standardised classification or operational definitions essential. Classifications are always incomplete and are amended over time as disciplines mature. In this regard, we suggest that the term 'turf' does not provide a common basis on which we can currently understand their identity and ecology. The term has such broad usage that it is in danger of becoming equivalent to a 'panchreston' which describes too much and explains too little (sensu Hardin 1956). This review does not seek to narrow the present usage of the term or provide a definition that is too restrictive. Rather, it seeks to encourage more objective and effective descriptions of 'turfs' that provide a common basis for comparison through the recognition and separation of critical differences (e.g. morphology and ecology) that may otherwise confuse comparisons.

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LITERATURE CITED

Abbott IA, Huisman JM (2004) Marine green and brown algae of the Hawaiian Islands. Bishop Museum Press, Honolulu, HI

Airoldi L (1998) Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79:2759–2770

Airoldi L (2001) Distribution and morphological variation of low-shore algal turfs. Mar Biol 138:1233–1239

Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. Oceanogr Mar Biol Annu Rev 41:161–236

Airoldi L, Virgilio M (1998) Responses of turf-forming algae to spatial variations in the deposition of sediments. Mar Ecol Prog Ser 165:271–282

Airoldi L, Rindi F, Cinelli F (1995) Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment influenced, rocky subtidal shore. Bot Mar 38:227–237

Airoldi L, Balata D, Beck MW (2008) The Gray Zone: relationships between habitat loss and marine diversity and their applications in conservation. J Exp Mar Biol Ecol 366:8–15

Airoldi A, Connell SD, Beck MW (2009) The loss of natural habitats and the addition of artificial substrata. In: Wahl M (ed) Marine hard bottom communities: patterns, dynamics, diversity and change. Book 206. Springer, Berlin, p 269–280

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150

Blockley DJ, Chapman MG (2008) Exposure of seawalls to waves within an urban estuary: effects on intertidal assemblages. Austral Ecol 33:168–183

Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30:381–390

Braun-Blanquet J (1932) Plant sociology: the study of plant communities. Stechert-Hafner Service Agency, New York, NY

Britton-Simmons KH (2006) Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. Oikos 113:395–401

Bulleri F, Benedetti-Cecchi L (2006) Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. Oecologia 149:482–492

Carpenter RC (1990) Mass mortality of *Diadema antillarum* I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Mar Biol 104:67–77

Connell SD (2007) Water quality and the loss of coral reefs and kelp forests: alternative states and the influence of fishing. In: Connell SD, Gillanders BM (eds) Marine ecology. Oxford University Press, Melbourne, p 556–568

Connell SD, Irving AD (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. J Biogeogr 35:1608–1621

Connell SD, Russell BD (2010) The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proc R Soc Lond B Biol Sci 277:1409–1415

Connell SD, Kroeker KJ, Fabricius KE, Kline DI, Russell BD (2013) The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance. Philos Trans R Soc Lond B Biol Sci 368:20120442

Corradini P, Clement B (1999) Growth pattern and modular reiteration of a hardy coloniser *Polytrichum commune* Hedw. Plant Ecol 143:67–76

Dahl AL (1972) Ecology and community structure of some tropical reef algae in Samoa. In: Nisizawa K (ed) Proc 7th Int Seaweed Symp. University of Tokyo Press, Tokyo, p 36–39

Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026–2033

Diaz-Pulido G, Villamil L, Almanza V (2007) Herbivory effects on the morphology of the brown alga *Padina boergesenii* (Phaeophyta). Phycologia 46:131–136

Edwards MS (1998) Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). J Exp Mar Biol Ecol 228:309–326

Foster MS (1972) The algal turf community in the nest of the ocean goldfish (*Hypsypops rubicunda*). Proc Int Seaweed Symp 7:55–60

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gislén T (1930) Epibioses of Gullmar Fjord II. Marine sociologi (Kristinebergs Zoologiska Station 1877–1927). Skriftserie K, Vol 4. Svenska Vetenskapsakademien, Stockholm

Gorman D, Connell SD (2009) Recovering subtidal forests on human-dominated landscapes. J Appl Ecol 46:1258–1265

Gorman D, Russell BD, Connell SD (2009) Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts. Ecol Appl 19:1114–1126

Hardin G (1956) Meaninglessness of the word protoplasm. Sci Mon 82:112–120

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Biol Ecol 69:61–84

Hauri C, Fabricius KE, Schaffelke B, Humphrey C (2010) Chemical and physical environmental conditions underneath mat- and canopy-forming macroalgae, and their effects on understorey corals. PLoS ONE 5:e12685

Hay ME (1981) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62:739–750

Irving AD, Connell SD (2006) Predicting understorey structure from the presence and composition of canopies: an assembly rule for marine algae. Oecologia 148: 491–502

Kelaher BP (2002) Influence of physical characteristics of coralline turf on associated macrofaunal assemblages. Mar Ecol Prog Ser 232:141–148

Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of sediment scour, erosion and accretion. J Exp Mar Biol Ecol 147:47–63

Kühnemann O (1970) Algunas consideraciones sobre los bosques de *Macrocystis pyrifera.* Physis 29:273–296

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12:474–478

Lauret M (1974) Etude phytosociologique préliminaire sur les gazon à *Pteosiphonia pennata* (Rhodophycées, Céramiales). Bull Soc Phycol Fr 19:229–237

McConnico L, Foster MS (2005) Population biology of the intertidal kelp, *Alaria marginata* Postels & Ruprecht: a non-fugitive annual. J Exp Mar Biol Ecol 324:61–76

McCook LJ (2001) Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs 19:419–425

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417

Moore JW (1974) Benthic algae of southern Baffin Island 3. Epilithic and epiphytic communities. J Phycol 10: 456–462

Murray S, Bray R (1993) Benthic macrophytes. In: Dailey MD, Reish DJ, Anderson JW (eds) Ecology of the Southern California Bight: a synthesis and interpretation. University of California Press, Berkeley, CA, p 304–368

Neumann AC, Gebelein CD, Scoffin TP (1970) The composition, structure and erodability of subtidal mats, Abaco, Bahamas. J Sediment Petrol 40:274–297

Neushul M, Dahl AL (1967) Composition and growth of subtidal parvosilvosa from California kelp forest. Helgol Wiss Meeresunters 15:480–488

Nikolic V, Zuljevic A, Antolic B, Despalatovic M, Cvitkovic I (2010) Distribution of invasive red alga *Womersleyella setacea* (Hollenberg) RE Norris (Rhodophyta, Ceramiales) in the Adriatic Sea. Acta Adriat 51:195–202

Norton TA, Fetter R (1981) The settlement of *Sargassum muticum* propagules in stationary and flowing water. J Mar Biol Assoc UK 61:929–940

Perkol-Finkel S, Airoldi L (2010) Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic sea. PLoS ONE 5:e10791

Piazzi L, Cinelli F (2000) Effects of the spread of the introduced Rhodophyceae *Acrothamnion preissii* and *Womersleyella setacea* on the macroalgal community of *Posidonia oceanica* rhizomes in the western Mediterranean Sea. Cryptogam Algol 21:291–300

Schiel DR, Thompson GA (2012) Demography and population biology of the invasive kelp *Undaria pinnatifida* on shallow reefs in southern New Zealand. J Exp Mar Biol Ecol 434-435:25–33

Steneck RS (1988) Herbivory on coral reefs: a synthesis. Proc 6th Int Coral Reef Symp, Townsville 1:34–79

Stewart JG (1982) Anchor species and epiphytes in intertidal algal turf. Pac Sci 36:45–59

Stewart JG (1983) Fluctuations in the quantity of sediments trapped among algal thalli on intertidal rock platforms in southern California. J Exp Mar Biol Ecol 73:205–211

Taylor PR, Hay ME (1984) Functional morphology of intertidal seaweeds: adaptive significance of aggregate vs. solitary forms. Mar Ecol Prog Ser 18:295–302

Virgilio M, Airoldi L, Abbiati M (2006) Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. Coral Reefs 25:265–272

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. In: Gibson RN, Atkinson RJA (eds) Oceanography and marine biology, Vol 41. Taylor & Francis, London, p 279–309

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